

CHAPTER 8-2

NUTRIENT RELATIONS: CO₂

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CHAPTER 8-2

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Figure 1. Peat moss, *Sphagnum fimbriatum*, covering the largest area of carbon sink in the world. Photo by Michael Lüth, with permission.

CO₂ Sources and Limitations

Early Carbon Relations

Colonization of life on the land of Earth began billions of years ago (Graham *et al.* 2014). Evidence suggests that bacteria, then **eukaryotic** (having a nucleus) algae, then bryophytes ventured to endure those early conditions. These early forms made possible the development of the first organic soils. To understand this progression and continuation of life, it is prudent to understand carbon cycling. For most terrestrial plants and algae, the source of this carbon is carbon dioxide (CO₂). Both green algae and bryophytes produce a degradation-resistant form of carbon from that CO₂ that is consequently sequestered. This, in turn, reduces the CO₂ in the atmosphere, having an important impact on the Earth's carbon cycle for 40-100 million years.

This early atmosphere was high in CO₂ compared to levels today (Raven & Edwards 2014). Isotope comparisons using liverwort fossils indicate that in the mid-Cretaceous in the Antarctic, CO₂ concentrations ranged 1000-1400 ppm, agreeing generally with

independent proxy data and long-term carbon cycle models (Fletcher *et al.* 2005). Furthermore, the concentration gradient from the atmosphere to the carboxylase in the plant would further drive CO₂ into the plant (Raven & Edwards 2014). This additional CO₂ would permit higher photosynthetic rates per surface area of plant. Later adaptations included increasing the surface area of photosynthetic tissue through development of complex structures and air spaces to permit greater harvesting of light.

Proctor (2010) suggested that in the early atmosphere of plant evolution in the mid-Palaeozoic, the atmosphere had 10X its present concentration of CO₂. It is thus unlikely that these early plants were CO₂ limited. Rather they may have increased their cuticularization, then increased their air spaces to permit them to take up more CO₂ and compensate for the blockage by the cuticle.

Relationships Today

In 1958, the CO₂ in the atmosphere had a concentration of 315 ppm (Scripps CO₂ Program 2016). In December

2016 it had grown to 404 ppm. Elbert *et al.* (2012) estimated that cryptogams (including Cyanobacteria, algae, fungi, lichens, and bryophytes) extract ~3.9 Pg carbon per year, or around 7% of the net production of terrestrial vegetation. Thus, the CO₂ uptake by bryophytes is an important component of global carbon cycling and a necessary contributor to climate modelling.

Normally we don't think of carbon as a limiting resource, although experiments on higher plants have shown that increased carbon dioxide usually increases productivity. Mosses are typically **C₃ plants** with high **CO₂ compensation points** (CO₂ concentration at which net CO₂ fixation is zero) (Raven *et al.* 1998). In other words, they require high levels of CO₂ to balance the CO₂ lost to respiration. **C₃ plants** are those plants that have no special mechanism for storing carbon from CO₂ temporarily in a compound such as **malate** or **oxalate**. Instead, they put all their CO₂ directly into the photosynthetic pathway in a 3-carbon compound, hence the term C₃. This pathway is less efficient because the enzyme **Rubisco** (Ribulose biphosphate carboxylase/oxidase) is much less effective at binding the atmospheric CO₂ into a 3-C compound within the cell than is **PEP carboxylase**, the enzyme used in the C₄ and CAM pathways to put the carbon in temporary storage C₄ compounds for later use in photosynthesis. However, mosses are not limited by guard cell closure in obtaining CO₂ and thus should be able to obtain CO₂ any time of the day.

In examining 32 terrestrial C₃ plants, Bauer and Martha (1981) found an average CO₂ compensation point of 36.2 µl L⁻¹ (=71 mg m⁻³). However, among these two mosses showed a somewhat higher CO₂ compensation point of ~43 µl L⁻¹. The compensation point for tracheophytes ranged 31-40 µl L⁻¹. Bain and Proctor (1980) found that the CO₂ compensation point of the aquatic bryophytes they studied were over 100 times higher than those of the C₃ aquatic tracheophyte *Elodea* and the alga *Chara*. They were likewise somewhat higher than those of terrestrial bryophytes reported by Dilks (1976).

Among tracheophytes, CAM plants, convert CO₂ to malate at night and store it to be used in the daytime, permitting the plants to conserve water by keeping stomata closed in the daytime. In C₄ plants a bundle sheath permits plants to convert CO₂ to a 4-carbon compound for use later. This likewise permits the plants to conserve water by closing stomata when the air is dry but to continue using CO₂ derived from the stored 4-C compounds for photosynthesis.

Bryophytes must live in a delicate balance between sufficient moisture and sufficient CO₂. When leaves are wet on the outside, that water offers significant resistance to CO₂ diffusion. Surprisingly, a thin cuticle permits greater diffusion than even a thin film of water, so mosses living in very wet habitats often are protected from waterlogging by well-developed waxes or other cuticular material (Proctor 1984). *Polytrichum commune* (Figure 2) and *P. strictum* (Figure 3) are good examples of this, but less obvious examples are *P. wahlenbergii* (Figure 4), *Pohlia cruda* (Figure 5), *Philonotis* (Figure 6), *Schistostega pennata* (Figure 7), *Saelania glaucescens* (Figure 8), and *Bartramia pomiformis* (Figure 9), all with a whitish appearance to the naked eye (Proctor 1984).



Figure 2. *Polytrichum commune* showing its somewhat waxy leaves. Photo by Michael Lüth, with permission.



Figure 3. *Polytrichum strictum* showing waxy leaves. Photo by Janice Glime.



Figure 4. *Pohlia wahlenbergii* var. *glacialis* showing its whitish color due to a thin cuticle. Photo by Michael Lüth, with permission.



Figure 5. *Pohlia cruda* showing its whitish color due to a thin cuticle. Photo by Michael Lüth, with permission.



Figure 6. *Philonotis fontana* showing its waxy leaves. Photo by Michael Lüth, with permission.



Figure 7. *Schistostega pennata* showing waxy leaf surface. Photo courtesy of Martine Lapointe.



Figure 8. Waxy-looking leaves of *Saelania glaucescens*. Photo by Ivanov, with permission.



Figure 9. *Bartramia pomiformis* showing waxy leaves. Photo by Jan-Peter Frahm, with permission.

Sphagnum (Figure 1) partially solves this balance by having water-holding cells (**hyaline cells**) that bathe the photosynthetic cells (Figure 10), while exposing at least one surface (in most) of the photosynthetic cell to the atmosphere. Furthermore, air bubbles become trapped among the leaves and between the leaves and the stem, thus providing an additional source of CO₂. Robinson (1985) considered that no CO₂ was obtained from the **hyaline** (water-holding) cells because all the chloroplasts of the cells were positioned along the wall most exposed to light. On the other hand, members of *Leucobryum* (Figure 11-Figure 14) do indeed trap air bubbles in their colorless cells (Robinson 1985), providing an internal source of CO₂ for the chlorophyllous cells residing there and causing these plants to somewhat mimic the internal structure of a seed plant. This same character seems to be present throughout the *Leucobryaceae* family, permitting their multi-layered leaves to function photosynthetically.

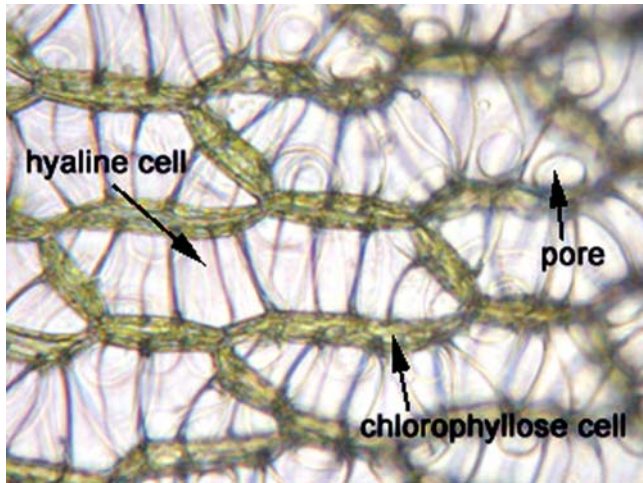


Figure 10. *Sphagnum* cells indicating the hyaline cells with pores, holding water, and chlorophyllose (photosynthetic) cells exposed to atmosphere. Photo with from Botany Website, UBC, with permission.



Figure 11. *Leucobryum glaucum* showing whitish color caused by hyaline cells that surround the photosynthetic cells. Photo by David T. Holyoak.

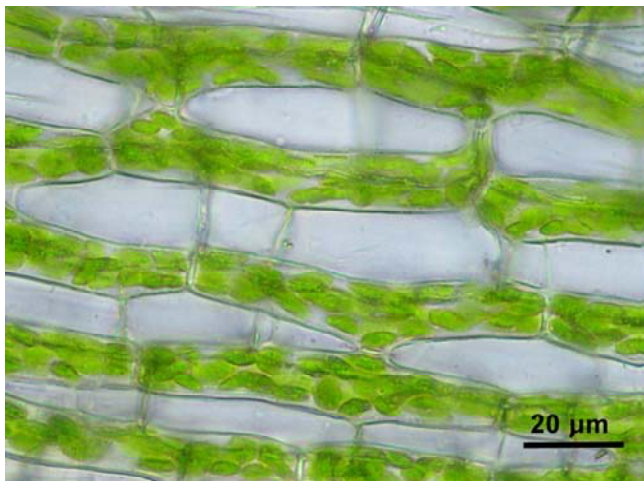


Figure 12. *Leucobryum glaucum* leaf cells in lamina view, showing hyaline and photosynthetic cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.



Figure 13. *Leucobryum glaucum* leaf cross section showing the photosynthetic cells surrounded by hyaline cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.



Figure 14. Whitish leaves due to hyaline cells of *Leucobryum juniperoideum*. Photo by Michael Lüth.

Shinde *et al.* (2015) determined that the moss *Physcomitrella patens* (Figure 15) has 814 genes that are affected by elevated CO₂ (1500 ppmV). These affect transcriptional reprogramming, photosynthetic regulation, carbon metabolism, and stress responses. CO₂ relationships are not simple!



Figure 15. *Physcomitrella patens*, demonstrating its whitish appearance due to a thin cuticle. Photo by Michael Lüth, with permission.

Structural Adaptations

Proctor (2010) explains that the maximum rate of CO₂ diffusion is limited by the difference between the external CO₂ concentration and the CO₂ **compensation point** (level of O₂ at which respiration = photosynthesis), as well as the resistance of the moist external bryophyte cell wall to the liquid-phase diffusion of the CO₂. This is limited by the thickness of the external cell walls. Structural differences can increase the plant uptake. A large, simple thallose liverwort provides a single flat photosynthetic surface. This is improved in an epiphyte such as *Metzgeria* (Figure 16) that exposes both surfaces. *Marchantia* (Figure 17) further increases the uptake surface by its system of internal chambers with photosynthetic cells arranged like tissues of a sponge (Figure 18).



Figure 16. *Metzgeria furcata* showing thalli exposed on both sides, thus doubling its CO₂-absorbing surfaces. Photo by Michael Lüth, with permission.



Figure 17. *Marchantia polymorpha* pores and gemmae cups. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

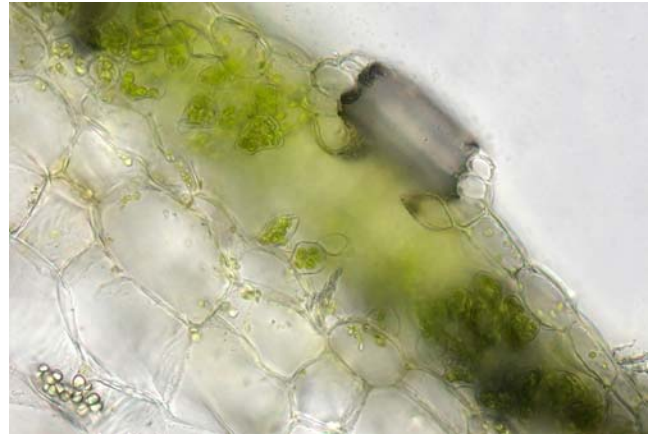


Figure 18. *Marchantia polymorpha* cs showing pore and underlying spongy chlorophyllose cells. Photo by Walter Obermayer, with permission.

Perhaps the most obvious adaptation of plants to intake of CO₂ is having stomata in leaves. This apparatus permits tracheophyte leaves to regulate moisture concentration in the leaves. However, when they are closed to conserve water, they are also closed to atmospheric CO₂ that is vitally needed for photosynthesis. Mosses and leafy liverworts lack stomata in their leaves, but generally have leaves that are only one cell thick, thus exposing two sides of the cell for absorption of CO₂. Some thallose liverworts, on the other hand, have a plant body that consists of multiple layers. These typically have a chambered interior with sponge-like tissues that provide lots of surface area. For these to obtain atmospheric CO₂, the chambers connect to the exterior atmosphere through pores that permit its diffusion into the chamber. Raven (2002) suggested that "stomata evolved from pores in the epidermis of plant organs which were at least three cell layers thick and had intercellular gas spaces and a cuticle."

But does this sponge-like interior make a difference? Meyer *et al.* (2008) demonstrated that both external and internal conductances, as well as water use efficiency, were higher in the ventilated (spongy) liverworts and hornworts. Within these two taxonomic groups, however, the values were similar, suggesting that various factors must serve to optimize the involved species for that life form.

Soil CO₂

Šimůnek and Suarez (1993) modelled the CO₂ transport and production in soil. CO₂ can be transported in the unsaturated zone in both the liquid and gas form. Both root and microbial respiration contribute to soil CO₂. The rate of this respiration is affected by water content, temperature, growth, salinity, and plant and soil characteristics.

In a temperate rainforest of New Zealand, bryophytes form a nearly continuous cover (62%) on the forest floor, with a depth less than 30 mm (DeLucia *et al.* 2003). The CO₂ was elevated relative to the atmosphere, presumably due to bacterial and fungal respiration. The net CO₂ exchange was very dependent on water content. Although the CO₂ uptake was quite variable, the annual net carbon uptake by the forest floor bryophytes was 103 g m⁻², compared to annual loss of carbon from the forest floor (bryophyte and soil respiration) of -1010 g m⁻². This

accounted for a reclamation of ~10% of the forest floor CO₂ emitted by respiration.

Tarnawski *et al.* (1994) measured 24-hour changes in atmospheric CO₂ concentrations within and above cryptogam stands in a New Zealand temperate rainforest. They found that CO₂ levels within the forest exceeded those in the open by 30 ppm and had a more variable **diel** (denoting a period of 24 hours) pattern (up to 70 ppm). The mean CO₂ level at a depth of 25 mm in the moss layer was 50% higher than those in the clearing and were higher than in the air of the rainforest.

In the Arctic tundra, there are definite differences in soil respiration rates related to microscale topography, mainly due to differences of soil water table and soil temperatures (Sommerkorn *et al.* 1999). The moss layer serves as a high impact modifier of the CO₂ emission, assimilating 51% to 98% of the daily amount CO₂ released from wet tundra soils.

For most forest floor mosses, the CO₂ should be ample to supply the slow-growing mosses due to production of CO₂ from litter decay. In the tropics, the CO₂ concentrations on the forest floor are greater than those above the canopy (Holtum & Winter 2001), but that enriched supply is still limiting. At 10 cm above the soil the CO₂ level is somewhat higher.

Because CO₂ is often limiting, even in the terrestrial system, increasing levels of CO₂ on the Earth could positively affect the bryophytes. Strain and Cure (1985) reported that the rate of photosynthesis in tracheophytes increases with a rise of atmospheric CO₂. Because bryophytes are C₃ plants, they are able to take advantage of high CO₂ levels. The increased temperatures that accompany the higher CO₂ through the greenhouse effect will cause greater below ground respiratory processes of roots, bacteria, and other organisms (Heal 1979; Silvola 1985). Bryophytes on the soil surface are the first photosynthetic organisms to have an opportunity to use this increased CO₂. Csintalan *et al.* (1997) found a small, but significant increase in CO₂ uptake in the drought-tolerant moss *Syntrichia ruralis* (Figure 19) when grown in a concentration of 700 ppm compared to that at the ambient level at that time of 350 ppm.



Figure 19. *Syntrichia ruralis* hydrated, a species that benefits from higher levels of CO₂. Photo by Misha Ignatov, with permission.

Sonesson *et al.* (1992) were able to show that the boreal forest moss *Hylocomium splendens* (Figure 20-Figure 21) can adapt to higher ambient CO₂ concentrations and utilize higher CO₂. Increasing CO₂ levels to 600 ppm (compared to 350 ppm), resulted in a significant increase in its photosynthesis and growth (Sonesson *et al.* 1996). Botting and Fredeen (2006) similarly showed that CO₂ (430 ppm) was limiting to moss productivity on the sub-boreal forest floor in central British Columbia, Canada.



Figure 20. *Hylocomium splendens* showing its extensive cover in the boreal forest. Photo by Andrew Spink, with permission.



Figure 21. *Hylocomium splendens*, a species that can benefit from a higher CO₂. Photo by Chmee through Creative Commons.

CO₂-Concentrating Mechanisms

CO₂-concentrating mechanisms are familiar in tracheophytes. In tracheophytes, allowing CO₂ into the leaf through stomata means allowing water vapor out (Hanson *et al.* 2014). Even chloroplasts leak water as they allow CO₂ in because both require the same pore size.

Bryophytes have neither of these carbon-storing mechanisms and it seems that all bryophytes are C₃ plants. But it appears that at least some do have a means to concentrate CO₂ (Meyer *et al.* 2008). Like members of the green algae, many hornworts (*Anthocerotophyta*; Figure 22-Figure 23) have **pyrenoids** (protein bodies in chloroplasts of some algae and hornworts) associated with the chloroplasts (Hanson *et al.* 2002, 2014). These

pyrenoids are able to maintain a pool of dissolved inorganic carbon (DIC) of 19-108 nmol mg⁻¹ chlorophyll (Hanson *et al.* 2002).



Figure 22. *Anthoceros agrestis* (Anthocerotophyta), representing a phylum in which many members have pyrenoids. Photo by Michael Lüth, with permission.

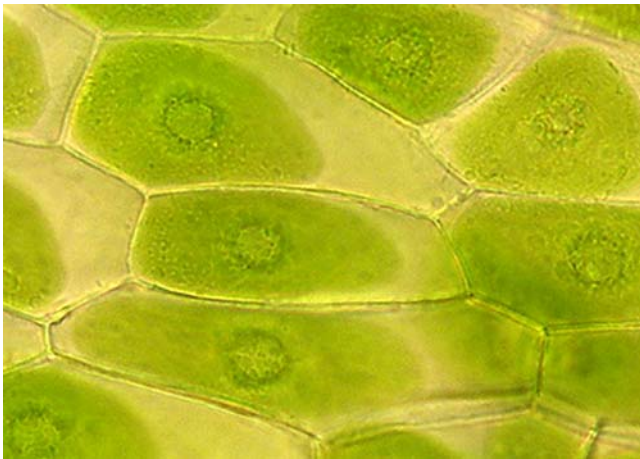


Figure 23. Hornwort (Anthocerotophyta) pyrenoids – the dark circles in the cells. Photo by Chris Lobban, with permission.

Villareal and Renner (2012) remind us of the important role of enzyme Rubisco (Ribulose-1,5-Biphosphate-carboxylase-oxygenase) in carbon fixation. But Rubisco is slow compared to PEP carboxylase, which they lack. These researchers noted that many scientists have hypothesized that carbon-concentration mechanisms evolved during periods of low CO₂ to concentrate CO₂ around the enzyme. But the cladistic analyses of Villareal and Renner do not support this hypothesis; pyrenoids have come and gone in the **Anthocerotophyta** (Figure 22-Figure 23) clades multiple times and do not always coincide with low CO₂.

Raven and coworkers (1998) have suggested that some aquatic mosses might have a "CO₂ concentrating mechanism" that differs from a typical C₃ pathway. The **Anthocerotophyta** use pyrenoids to accomplish CO₂ concentration, with the exception of *Megaceros* (Figure 24), in which there is no pyrenoid, but the mechanism in aquatic mosses is unknown. In evaluating a number of taxa, Raven's group found no evidence of C₄ or CAM pathways in bryophytes, but Salvucci and Bowes (1981) found that two aquatic taxa, *Fontinalis antipyretica* (Figure 25) and *Fissidens cf. mahatonensis*, seem to be

able to concentrate CO₂. What is even more interesting, it appears that it might be facultative. When they measured the CO₂ compensation point of *F. cf. mahatonensis* in the cool Florida winter (12°C, 10 h day length), the compensation point was consistent with that expected for a C₃ pathway. However, when they measured it for the hot Florida summer (30°C, 14 h day length), the CO₂ compensation point was much lower, although not as low as in a C₄ pathway. They found similar summer/winter CO₂ compensation point relationships in all the aquatic bryophytes tested from Florida. This would be a very beneficial adaptive feature since the CO₂ is easily lost from water at high temperatures. The Section below on Aquatic CO₂ will detail what we know about obtaining CO₂ in water.



Figure 24. *Megaceros* (Anthocerotophyta), a genus that lacks pyrenoids. Photo by Juan Larrain, with permission.



Figure 25. *Fontinalis antipyretica*, an aquatic moss that must get its CO₂ from that dissolved in water. Photo by Andrew Spink, with permission.

Bryophytes may be able to use fixed carbon compounds that are different from those used by tracheophytes. Simola (1969) experimented with *Sphagnum nemoreum* (syn of *S. capillifolium*; Figure 26) in sterile culture and found that whereas mannose [hexose monosaccharide (6-carbon sugar) with a structure very similar to glucose] and its 6-carbon derivative, rhamnose, are toxic to many flowering plants, mannose promotes the growth of *Sphagnum nemoreum*. On the other hand, other common sugars such as arabinose, galactose, ribose, and

xylose are toxic to *Sphagnum*. While the literature is not as complete as that on tracheophytes, we know that at least *Funaria hygrometrica* (Figure 27) can use the sugars fructose, glucose, maltose, and sucrose as internal carbon compounds (Simola 1969).



Figure 26. *Sphagnum capillifolium* (*nemoreum*), a species for which **mannose** promotes growth. Photo by Bernd Haynold, through Creative Commons.



Figure 27. *Funaria hygrometrica* with young sporophytes, a species that can use the sugars fructose, glucose, maltose, and sucrose internally. Photo by Andrew Spink, with permission.

Further evidence of differences in carbon usage by *Sphagnum* come from studies on carbon isotope discrimination. In three species that occupy hollows (*S. recurvum* – **Error! Reference source not found.**), carpets (*S. palustre* – Figure 29), and hummocks (*S. tenerum*), the delta ¹³C values (indicating their ability to discriminate CO₂ on the basis of the ¹²C or ¹³C isotope) ranged from 19.0 to 27.1, but were unrelated to species (Rice 2000). Rather, they differed significantly ($p < 0.001$) with season. In the spring, discrimination was lower (mean 22.5), with the highest discrimination in winter (24.7). This difference was mainly due to low photosynthetic rates in winter that reduce the effects of diffusional resistance on carbon isotope discrimination. Microhabitat differences that were present in the field disappeared in the common garden and eliminated any doubt about species differences in ability to discriminate. The observed seasonal differences in carbon isotope discrimination appear to be different from those of

tracheophytes, where water limitation lowers chloroplastic demand and increases resistance to C uptake. In *Sphagnum*, water limitation lowers the chloroplastic demand but also decreases the resistance to C uptake, suggesting that the moss continues to incorporate carbon as it dries.



Figure 28. *Sphagnum recurvum*, a species of hollows. Photo by Tryon Life Community Farm, through Creative Commons.



Figure 29. *Sphagnum palustre*, a species of carpets. Photo by Bernd Haynold, through Wikimedia Commons.

Carbon isotope ratios have been used for dating all sorts of biological materials, including the age of peatlands. Using carbon isotope technology, MacDonald *et al.* (1987) found that peatland mosses consistently registered carbon ages that were considerably older than those of the macrofossils of the same layer. They found ages that ranged 1400 to 6400 years older than that of their contemporary tracheophytes, and even the live *Drepanocladus crassicoatus* had a ¹⁴C content that was only 85% that of other present-day taxa. They explained this moss phenomenon as an isotope exchange with older sediments, the formation of CO₂ from bicarbonate by chemical processes, and the metabolic production of CO₂, presumably including bacterial decomposition, especially by mycobacteria.

Aquatic CO₂

In aquatic systems, CO₂ is not very soluble, is easily lost to the atmosphere at warm temperatures, and availability is pH-dependent, so it can indeed be limiting. The diffusion coefficient for CO₂ in water is only 10⁻⁴ times that found in air. The boundary layer between the moss and the flowing water reduces that availability even more. Aquatic bryophytes have high CO₂ compensation points (> 50 µl L⁻¹), higher than that of typical of C₃ tracheophytes (Bain & Proctor 1980).

Raven *et al.* (1998) indicate that stream mosses such as *Fontinalis antipyretica* (Figure 25) have very little CO₂ limitation because of the constantly flowing water that renews CO₂ and the reduced boundary layer resulting from water flow. On the other hand, in deep, quiet water, this species has much more difficulty getting CO₂, despite higher concentrations, due to the increased boundary layer surrounding the moss.

Unlike many aquatic tracheophytes, mosses are apparently unable to use bicarbonates as a source of CO₂ (Bain & Proctor 1980; Allen & Spence 1981). Ruttner (1947) first demonstrated this limitation quantitatively in the mosses *Calliergon giganteum* (Figure 30), *Cratoneuron filicinum* (Figure 31), *Eucladium verticillatum* (Figure 32-Figure 33), *Fissidens rufulus* (Figure 34-Figure 35), *Hylocomium splendens* (Figure 20-Figure 21), and *Neckera crispa* (Figure 36) and the thallose liverwort *Marchantia polymorpha* (Figure 17), and Steeman Nielsen (1947) found the same in *Fontinalis antipyretica* (Figure 25), even though *F. antipyretica* has the enzyme carbonic anhydrase needed for the conversion of bicarbonate to CO₂. Bain and Proctor (1980) further examined mosses from alkaline habitats, yet were unable to demonstrate any use at all of bicarbonates; Allen and Spence (1981) independently determined this once more for *Fontinalis antipyretica*.



Figure 30. *Calliergon giganteum*, a species that cannot use bicarbonate as a carbon source. Photo by Misha Ignatov, with permission.



Figure 31. *Cratoneuron filicinum*, a species that is unable to use bicarbonate as a carbon source. Photo by Barry Stewart, with permission.

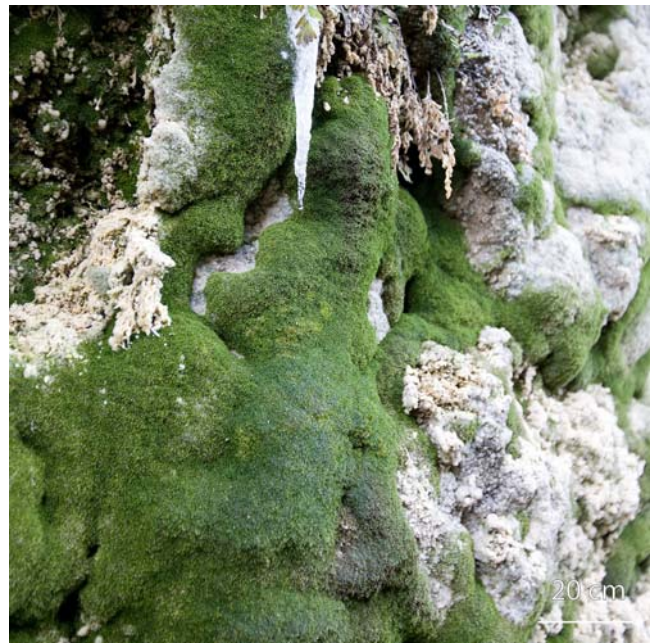


Figure 32. *Eucladium verticillatum* in its wet habitat. Photo by Proyecto Musgo, through Creative Commons.



Figure 33. *Eucladium verticillatum*, a species that is unable to use bicarbonates as a carbon source. Photo by Barry Stewart, with permission.

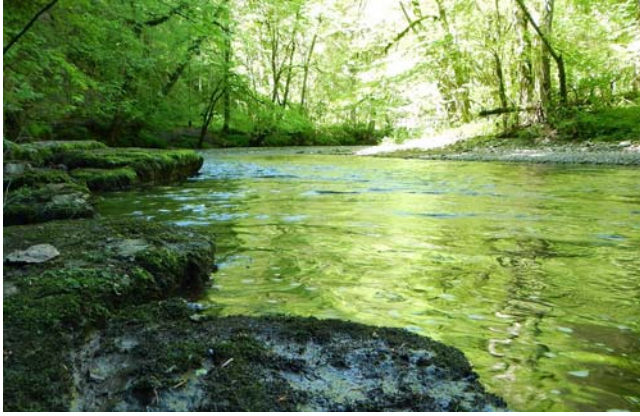


Figure 34. *Fissidens rufulus* habitat. Photo by Michael Lüth, with permission.



Figure 35. *Fissidens rufulus*, a species that is unable to use bicarbonate as a carbon source. Photo by Michael Lüth, with permission.



Figure 36. *Neckera crispa*, a species that is unable to use bicarbonate as a carbon source. Photo by Barry Stewart, with permission.

Therefore, in aquatic systems at higher levels of pH, when the CO₂ equilibrium shifts toward bicarbonate or carbonate, CO₂ becomes unavailable. In these conditions, perhaps the CO₂ is transformed from bicarbonates in some taxa by lower pH values at the moss-water interface, but no experimental evidence has verified this hypothesis. Thus, the number of mosses growing in alkaline waters is limited, and it seems that many of the ones that do occur in alkaline

waters are adapted to growing in the highly aerated water of waterfalls and rapids, as, for example, *Fissidens grandifrons* (Figure 37) (pers. obs.). Some grow in very cold glacial meltwater in which more CO₂ is soluble (Vitt *et al.* 1986). Others are restricted to the splash zone at the edge of the water, where CO₂ is trapped as the water moves through the air, as in *Cratoneuron* (Figure 38) species (Vitt *et al.* 1986; Glime & Vitt 1987).

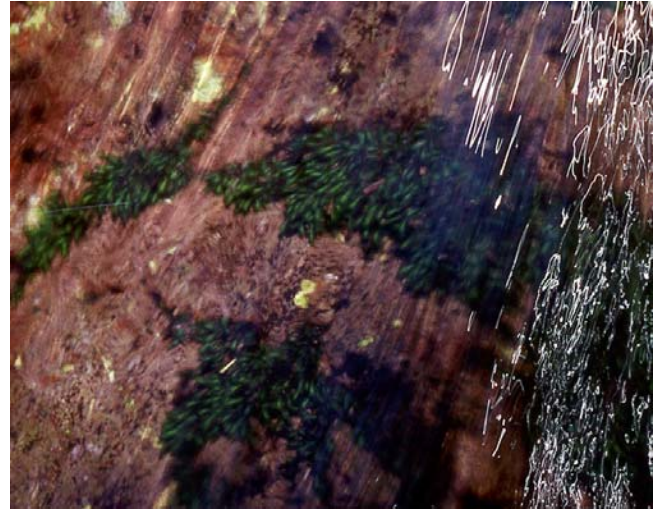


Figure 37. *Fissidens grandifrons*, in fast-flowing water where there is more CO₂ than in quiet water. Photo by Janice Glime.



Figure 38. *Cratoneuron commutatum* var *fluctuans* at the edge of water. Photo by Michael Lüth, with permission.

When mosses live at great depths, light and temperature can be low. The ability of mosses to grow slowly reduces their need for CO₂ and light. In great depths of Lake Grane Langos, Denmark, *Sphagnum subsecundum* (Figure 39) and *Drepanocladus exannulatus* (Figure 40) grew faster in deep water than in shallow water! (Riis & Sand-Jensen 1997). Riis and Sand-Jensen concluded that this more rapid growth at greater depths was possible due to lower temperatures that permitted more CO₂ to remain dissolved, CO₂ supersaturation, and nutrient enrichment from the sediments below the thermocline.



Figure 39. *Sphagnum subsecundum*, a species that takes advantage of CO₂ supersaturation in deep water. Photo by Michael Lüth, with permission.



Figure 40. *Drepanocladus exnnulatus*, a species that takes advantage of CO₂ supersaturation in deep water. Photo by Michael Lüth, with permission.

Role of pH

In the aquatic system, pH is important in determining the chemical fate of the CO₂. Under acidic conditions, it remains dissolved as CO₂. But if the water is warm, the CO₂ gas is easily lost to the atmosphere.

At circum-neutral pH levels, the CO₂ in water is converted to bicarbonate. At least some tracheophytes are able to use bicarbonates, but studies on use by bryophytes are ambiguous. In basic waters, carbonates are formed and cannot be used by any of the plants.

In situations of higher pH, CO₂ can be present for a short time as it is released from sediments or trapped in turbulent water (Lovalvo *et al.* 2010). Bryophytes could take advantage of these ephemeral concentrations before they are converted to unusable forms.

Within the cell, the enzyme **carbonic anhydrase** converts bicarbonates to CO₂ in both bryophytes and tracheophytes (Steeman Nielsen & Kristiansen 1949; Arancibia & Graham 2003). Some tracheophytes use extracellular carbonic anhydrase to convert bicarbonates to free CO₂ (Allen & Spence 1981). There is no direct evidence that bryophytes can use bicarbonates (James 1928; Ruttner 1947; Steeman Nielsen 1947; Bain & Proctor 1980; Allen & Spence 1981; Osmond *et al.* 1981; Glime & Vitt 1984; Prins & Elzenga 1989; Madsen *et al.* 1993; Ballesteros *et al.* 1998; Raven *et al.* 1998); nevertheless,

some bryophytes are able to live in the pH range of bicarbonates. I have an unconfirmed suspicion that bryophytes may convert limited amounts of bicarbonate to CO₂ at the leaf surface, perhaps by the presence of H⁺ released from exchange sites.

To further complicate the story, Farmer *et al.* (1986) found that the aquatic moss *Fontinalis antipyretica* (Figure 25) has no **PEP carboxylase** and uses only Rubisco for its fixation of CO₂ in photosynthesis, supporting the earlier conclusion of Steeman Nielsen (1947) that *F. antipyretica* cannot use bicarbonates from the water for its photosynthesis. Nevertheless, Harder (1921) had already shown that *F. antipyretica* increased its net assimilation from 0.01 to 0.64% when bicarbonate concentration was raised from 0.66 to 3.14 as HCO₃⁻. Later, Burr (1941) likewise demonstrated greater productivity in this species in water with more bicarbonate than in that with CO₂. Steeman Nielsen and Kristiansen (1949) offered a possible explanation – that CO₂ might enter photosynthetic reactions in its hydrated form, *i.e.* as bicarbonate.

Bain and Proctor (1980) found that of the 20 aquatic species tested from a variety of habitats, all but the hornwort *Anthoceros husnotii* with pyrenoids had pH compensation points in the range expected for CO₂-dependent C₃ plants. Nevertheless, many studies support the concept that all aquatic mosses are C₃ plants (Ruttner 1947; Allen & Spence 1981; Osmond *et al.* 1981; Salvucci & Bowes 1981; Raven 1991; Raven *et al.* 1987, 1994, 1998), despite some living in conditions that have CO₂ concentrations below the expected CO₂ compensation point.

Peñuelas (1985) demonstrated what appeared to be use of NaHCO₃ (sodium bicarbonate) by *Fontinalis antipyretica* (Figure 25) as a carbon source. During photosynthesis by this species, the pH increased to 9.6, indicating a CO₂ compensation point of 1.1 mM m⁻³ CO₂. This photosynthetic rate was higher than could be explained by CO₂ alone and when HCO₃⁻ levels were increased, the photosynthetic rate likewise increased, even though CO₂ levels in the water were held constant. In fact, photosynthesis continued until the pH reached 11.8-12.0 for *F. antipyretica* and 10.10 for the alkaline-tolerant *Fissidens grandifrons* (Figure 37). But to further confuse the issue, in a different stream, Peñuelas found that *F. antipyretica* could not use HCO₃⁻ to photosynthesize, suggesting either different physiological races or different acclimation to conditions. We know that there are genetic differences among populations of this highly variable species (Shaw & Allen 2000). Even if these genetic differences are expressed as a physiological mechanism to use bicarbonate, we still do not understand what that mechanism might be!

Bogs

Hummocks present unique habitats, and their CO₂ relations are no exception. Rydin and Clymo (1989) described their upper parts as obtaining CO₂ from air rather than water between the *Sphagnum* (Figure 26) plants, depending on high CO₂ concentrations in the **acrotelm** (living layer of peat) water. In fact, they found that the CO₂ concentration in that layer was twice that in the outside atmosphere (Rydin & Clymo 1989; Smolders *et al.* 2001).

As the atmospheric levels of CO₂ rise and N deposition provides critical and often limiting nutrients, the composition of plant communities changes. This is particularly true in *Sphagnum* (Figure 41-Figure 46) bogs (Berendse *et al.* 2001). In this case, we expect productivity of tracheophytes to increase as they benefit from greater CO₂, often decreasing the competitiveness of the bryophytes and causing tracheophyte expansion. *Sphagnum* is one of the most important groups of plants to serve as a carbon sink in the Northern Hemisphere, facilitated by its slow decomposition. But when Berendse and coworkers studied the effects of raised CO₂ and N on *Sphagnum* and other plants in four locations in Western Europe, the elevated CO₂ had no effect on *Sphagnum* biomass increase. N, on the other hand, caused a decrease in *Sphagnum* growth due to competition.

In a bog in the Netherlands, *Sphagnum magellanicum* (Figure 41) benefitted from elevated CO₂ by exhibiting increased growth in height in the second and third growing seasons (Heijmans *et al.* 2001). Tracheophytes that grew close to the more rapidly growing *S. magellanicum* were affected negatively by the increased *Sphagnum* height. Mitchell *et al.* (2002) found that on one harvested peatland the initial colonizer was *Polytrichum strictum* (Figure 3). Under a treatment of added CO₂ (560 ppm), the later colonizer *Sphagnum fallax* (Figure 42) was able to successfully compete with the *P. strictum*.



Figure 41. *Sphagnum magellanicum*, a species that increases in height growth when living in higher CO₂ levels. Photo by David Holyoak, with permission.



Figure 42. *Sphagnum fallax*, a species that competes better in an atmosphere with higher CO₂. Photo by Michael Lüth, with permission.

Van der Heijden *et al.* (2000a) found that not all *Sphagnum* had the same response to elevated CO₂. *Sphagnum papillosum* (Figure 43), an oligo-mesotrophic species, benefitted in growth from elevated CO₂ (720 ppm). On the other hand, the ombrotrophic *S. balticum* (Figure 44) received no growth benefit, despite elevated sugar in stems and capitula in both species. Unlike many of the studies discussed in subchapter 8-1, in this case additional N along with elevated CO₂ benefitted *S. papillosum*, but it had no effect on *S. balticum*. Doubling CO₂ without N addition cause lower N levels in both species.



Figure 43. *Sphagnum papillosum* with sundew. Photo by Michael Lüth.



Figure 44. *Sphagnum balticum*, a species that does not benefit when additional N accompanies elevated CO₂. Photo by Michael Lüth, with permission.

The response of *Sphagnum recurvum* var. *mucronatum* (Figure 45) may explain the elevated sugars (van der Heijden *et al.* 2000b). Initially, elevated CO₂ stimulated photosynthesis, but after 3 days of exposure it was down-regulated to pre-elevation values. However, the elevated CO₂ continued to cause reduced dark respiration. At the same time there was a continuous increase in soluble sugar in the capitula. Doubling the CO₂ caused a decrease of N in the capitula, but not in the stems. This N reduction was coupled with a decrease in amino acids but did not affect soluble protein levels, causing a shift in N partitioning.



Figure 45. *Sphagnum recurvum* var *mucronatum*, a species that stores elevated sugars when the CO₂ is elevated. Photo by Jan-Peter Frahm, with permission.

Not all *Sphagnum* grows in hummocks. *Sphagnum cuspidatum* (Figure 46) grows primarily submersed. When it was subjected to added CO₂ for 12 weeks, only the highest CO₂ concentration in the water caused increased growth in length and biomass (Paffen & Roelefs 1991).



Figure 46. *Sphagnum cuspidatum*, a submersed moss that is indifferent to added CO₂ until the levels are quite high. Photo by Michael Lüth, with permission.

In addition, some bryophytes may be able to tap into a source of carbon we usually don't consider in bryophytes. Rydin and Clymo (1989) have demonstrated that at least in *Sphagnum* the fixed carbon can be transported within the stem. Using ¹⁴C labelling on *Sphagnum papillosum* (Figure 43), they found almost the entire alcohol-soluble fraction moved from older parts to the apex, with little transfer of the insoluble fraction.

Methane

Methane (CH₄) is the product of **anaerobic** (no oxygen) bacterial breakdown. In several bogs of Canada, the highest emissions occurred in raised-bog and patterned-poor-fen pools where the peat is degrading (Bubier 1995). Methane is much more effective as a greenhouse gas compared to CO₂. And wetlands are the largest natural source for methane. Submerged *Sphagnum* (Figure 46) uses methane that is converted through symbiosis with partly endophytic **methanotrophic** (able to gain carbon

from methane) bacteria, leading to highly effective *in situ* methane recycling (Raghoebarsing *et al.* 2005). These bacteria live in the hyaline cells and on leaves where they convert the methane to CO₂. This conversion provides 10-15% of the carbon source for these *Sphagnum* species.

CO₂ and Desiccation Tolerance

Syntrichia ruralis (Figure 19) is a common desiccation-tolerant moss. When subjected to elevated CO₂ it showed increased net CO₂ uptake in high CO₂ conditions by more than 30% (Tuba *et al.* 1998). Both desiccation-tolerant and non-tolerant plants, bryophytes included, show initial positive responses of photosynthesis to elevated CO₂, but both groups exhibit reduced or even reversed photosynthetic rates in the longer term (Tuba *et al.* 1999). This slightly later study implies that increased CO₂ levels will have little advantage for either group of bryophytes.

Translocation

Rydin and Clymo (1989) found that carbon is transported within *Sphagnum* (Figure 45) plants. This could provide a physiological mechanism that moves older carbon compounds from deeper parts of the peatlands upward. This could dilute the ¹⁴C pool within the living plant and change both the location and the proportions of ¹²C, ¹³C, and ¹⁴C. If *Sphagnum* is able to take in carbon from deep sediments and move it upward in the water column, this would result in false readings for carbon dating. Might the moss be preferentially moving ¹²C upward from older peat and thus reducing its proportion of ¹⁴C? If so, we need to re-evaluate our methods for dating peat.

By contrast, it appears that mosses like *Grimmia* (Figure 47) that receive their water from above can actually move carbon as photosynthate from the tip of the plant to the base and even to underground parts, much as we would find in a tree (Alpert 1989). Lacking any specialized conducting cells, this moss presents a puzzle as to its mechanism of movement, although as we shall see later in this chapter, it uses the source-sink principle used by tracheophytes.

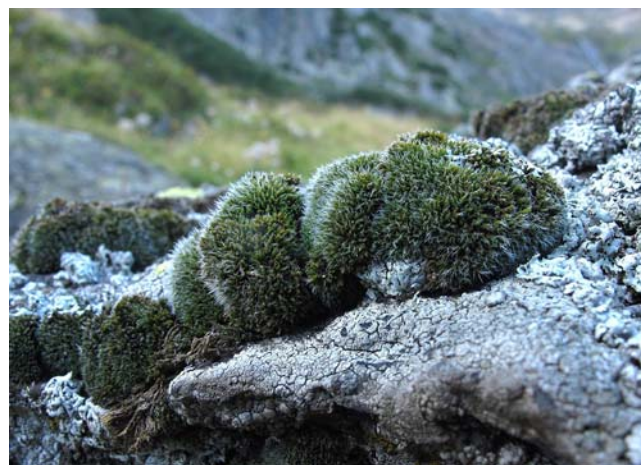


Figure 47. *Grimmia caespiticia*, a moss that moves photosynthetic carbon from the tip to the base. Photo by Michael Lüth, with permission.

Importance of Bryophytes in C Cycling

Porada *et al.* (2013) estimated that the terrestrial net uptake of carbon by bryophytes and lichens is 0.34 to 3.3 Gt yr⁻¹. This appears to be small until you consider bogs and Arctic habitats where bryophytes dominate the vegetation. In those location, the bryophytes are significant carbon sinks.

Summary

The early atmosphere had considerably more CO₂ than the current one. However, in the last 60 years, CO₂ concentrations have risen from 315 to 404 ppm in the atmosphere.

Soils release CO₂ through respiration by bacteria, fungi, and other soil organisms. Bryophytes are able to trap much of this CO₂ before it reaches the atmosphere.

Thallose liverworts may have a spongy interior with pores to facilitate exposure of internal photosynthetic cells to CO₂. Mosses are C₃ plants that benefit from high CO₂ concentrations and cool to moderate temperatures (up to 25°C). They have difficulty obtaining CO₂ when they are wet and the presence of cuticular waxes in species such as *Polytrichum* spp. and *Saellania glaucescens* facilitates the absorption of CO₂ by repelling water. *Sphagnum* keeps its photosynthetic cells moist on 2-3 sides while permitting 1-2 sides to be exposed to the atmosphere.

Hornworts may have pyrenoids that concentrate CO₂ around the enzyme Rubisco, facilitating photosynthesis. Some aquatic mosses may be able to concentrate CO₂ and this may be facultative, being enhanced on hot days. In acid conditions they use CO₂ dissolved in the water, but some evidence suggests that in the mid-pH range some species may be able to use bicarbonates.

Some bryophytes can use amino acids. At least some *Sphagnum* species use methane as a carbon source. And some species can move C up or down within the plant.

Bryophytes, especially in wet habitats, may be able to move water up from sediments, taking advantage of decompositional carbon. Others may move photosynthate from actively growing apical parts to lower parts for storage.

Bryophytes may serve as carbon sinks, especially in peatlands.

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